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GROWTH AND PRODUCTION OF THE DWARF SURF CLAM *MULINIA LATERALIS* (SAY 1822) IN A GEORGIA ESTUARY

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ABSTRACT The bivalve *Mulinia lateralis* is a dominant member of estuarine benthos, but its presence and abundance in Georgia estuarine waters is sporadic over time. Recruitment and production was monitored from 1977 through 1981 at three inner and one outer more saline ($>$ 18 ppt) areas of Wassaw Sound. Until the winter of 1981, *Mulinia lateralis* was absent or at very low densities. Significant settlement occurred in January 1981 when densities in the outer sound reached as high as 63,000 individuals • m^{-2} . The clam was more abundant in sandy mud ($\bar{x}$ = 10,161 • m^{-2}) than mud ($\bar{x}$= 277 • m^{-2}) or sand ($\bar{x}$= 263 • m^{-2}). Cohort production varied from 0.3 g dry wt • m^{-2} • 4 $months^{-1}$ in the inner sound to 325 g dry wt • m^{-2} • 7 $months^{-1}$ in the outer Sound, with the mean biomass ranging from 0.6 to 513 g dry wt • m^{-2}, respectively. When present, *Mulinia lateralis* contributes significantly to benthic production available to commercially valuable fish and crabs. That this food resource is annually and seasonally episodic could contribute to year-to-year fluctuations in production of species preying on benthos.

INTRODUCTION

The dwarf surf clam *Mulinia lateralis* (Say 1822) (Bivalvia; Mactridae) is a typical dominant member of estuarine benthos whose density characteristically fluctuates widely. Populations of this clam may dominate the benthos one year or part of a year, only to be absent the following year(s). Fluctuations in the abundance of benthos of Wassaw Sound, in Georgia (Fig. 1), may be in part caused by salinity depressions in winter/spring when many benthic species spawn (Walker et al. 1980, Walker and Tenore 1984). For example, *M. lateralis* and the northern hard clam *Mercenaria mercenaria* (Linné) did not settle significantly between 1977 and 1980, when low winter salinities resulted from heavy rainfall in upstate Georgia. Because of a drought in 1981, salinities were not depressed in winter/spring and a significant set of juveniles of *M. mercenaria* and *M. lateralis* occurred.

The contribution of *M. lateralis* to benthic production is especially important because this species, when present, is an important source of food for many commercially valuable fish and crabs (Brever 1957, Tagatz 1969, Virnstein 1977). Little information exists on the production of opportunistic species such as *M. lateralis*. We describe here the production of a single cohort age-class of *M. lateralis* following the 1981 set of this bivalve after several years of recruitment failure. Information was gained on the contribution of the clam to benthic production during a period of high clam density.

STUDY SITE

Wassaw Sound (Fig. 1) is a coastal estuarine embayment located in the Georgia Bight (Howard and Frey 1980). Semidiurnal tides average 2.4 m, with spring tides ranging approximately 3.4 m (Hubbard et al. 1979). Water temperatures (Dörjes 1972) and salinities at the mouth of the Sound (Howard and Frey 1980) range from 8°C and 20 ppt in the winter to 30°C and 30 ppt in the summer. Sediments range from silt-clay to fine sand with interbedded sand and mud the most prevalent (Howard and Frey 1975).

MATERIALS AND METHODS

Four stations (Fig. 1) were sampled monthly from January to December 1981 by taking six 0.05-m^2 van Veen grabs at each station. Samples were sieved through a 0.297-mm mesh and preserved in 10% formalin in sea water. Samples were returned to the laboratory, sorted under a dissecting scope and specimens of *M. lateralis* were counted and measured for shell length (longest possible measurement, i.e., anterior-posterior distance).

Station 1 was located in the Skidaway River approximately 1 mile south of the Skidaway Institute of Oceanography where the clams occurred in a muddy substrate in approximately 1.5 m of water at mean low water. Station 2 was located in the Wilmington River at the U.S. 80 drawbridge at Thunderbolt, Ga., where the clams occurred in a muddy substrate in approximately 0.5 m of water at mean low water. Station 3 was located at the junction of Skidaway and Wilmington rivers, where the clams occurred in a sandy mud substrate in approximately 2 m of water at mean low water. Station 4 was located in the Wilmington River near the junction of Wilmington and Cabbage islands, where the clams occurred in approximately 0.2 m of water at mean low water.

The shell-length to dry-weight (DW) relationship was determined for *M. lateralis* (n = 100). After clams were measured to the nearest mm, the flesh was removed and dried to constant dry weight at 80°C for 48 h.

Secondary production was calculated using the instantaneous growth model of Waters and Crawford (1973):

$$P = G\bar{B}$$

where P = production in grams • m^{-2} , G = instantaneous

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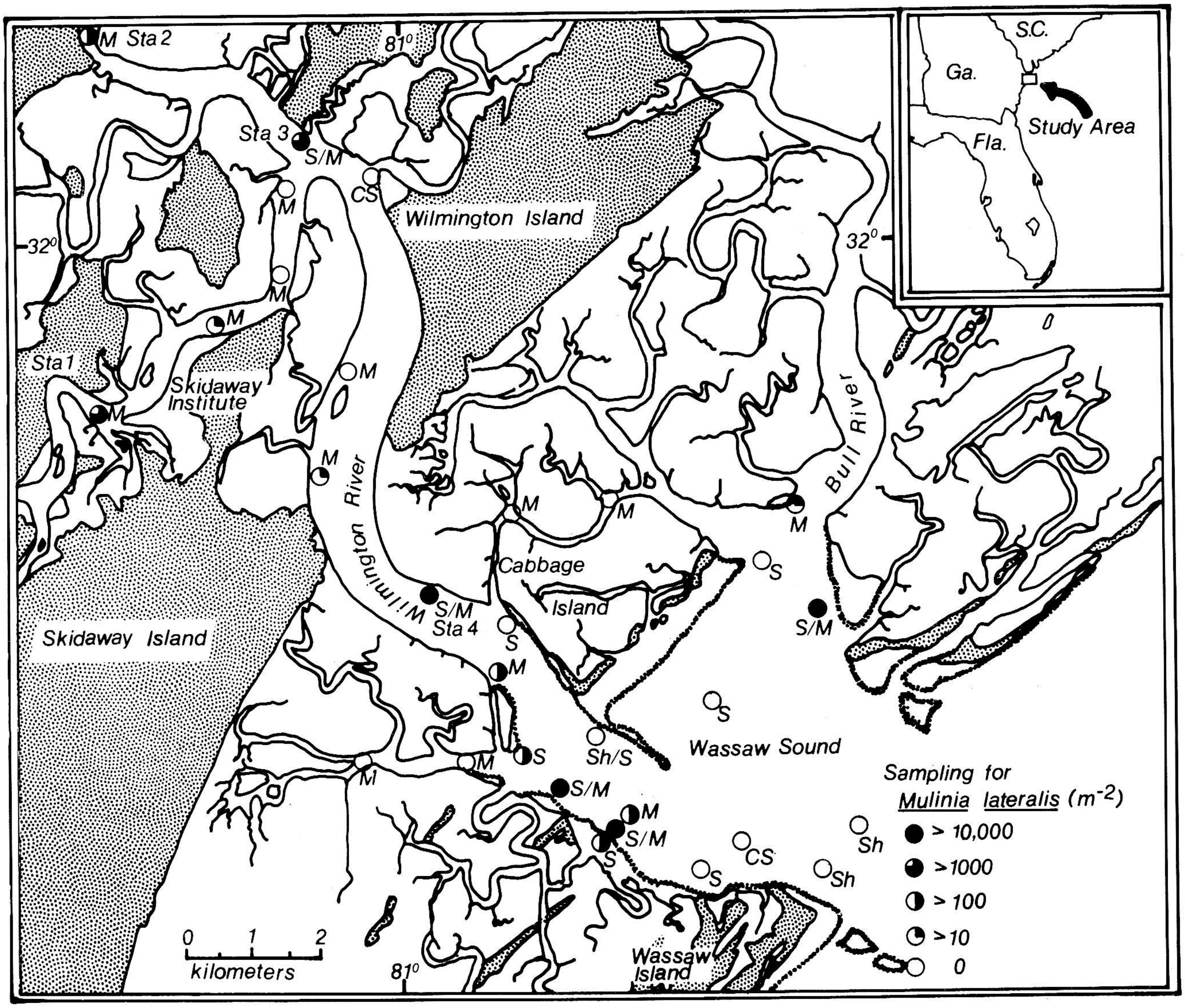

Figure 1. The distribution and relative abundance of *Mulinia lateralis* in Wassaw Sound, Georgia. Letters below the density symbols refer to substrate type: sh = shell, cs = coarse sand, s = sand, s/m = sandy mud, and m = mud.

growth for the time interval, and $\bar{B}$ = mean standing crop between given time intervals ($\bar{B} = [B_t + B_{t+1}]/2$). Instantaneous growth rate (G) is calculated as $\ln(W_t/W_o)$ where o and t represent the beginning and end of each time interval. Annual production is equal to the summation of the individual intervals' production estimates. Individual weights for the table were obtained by taking the mean of the clam lengths per month per station and applying that value to the shell-length to dry-weight regression equation.

Growth was determined by plotting the mean weight of the clams against time. Mean weights were determined using monthly mean shell lengths and converting to biomass.

RESULTS

Clams were absent or at low densities ($< 10 \cdot m^{-2}$) from 1977 to winter 1981. In January 1981 newly set clams were found throughout the Sound. Clams set intertidally to a depth of 7 m, with heaviest settings in the outer Sound (up to $63{,}000 \cdot m^{-2}$). Inshore of Skidaway and Wilmington islands, densities were $< 2000 \cdot m^{-2}$. Densities also varied with sediment type (Fig. 1). Clams had average densities of $10{,}161 \pm 19{,}475$ (SD) $\cdot m^{-2}$ in sandy mud, 277 ± 522 (SD) $\cdot m^{-2}$ in mud, 263 ± 468 (SD) $\cdot m^{-2}$ in sand, and were absent in coarse sand and shelly bottoms. In areas where the substrate changed from sand to mud, clams were more dense in the sand-to-mud interphase.

Densities increased at the four stations from January to February and then declined. Some specimens of *M. lateralis* in Wassaw Sound were mature and ripe in April but there was no new recruitment. None were found at Sta 1, 2, and 3 after April. Clams persisted at Sta 4 until August (Fig. 2). Densities varied greatly from a low of $525 \cdot m^{-2}$ at Sta 2 to

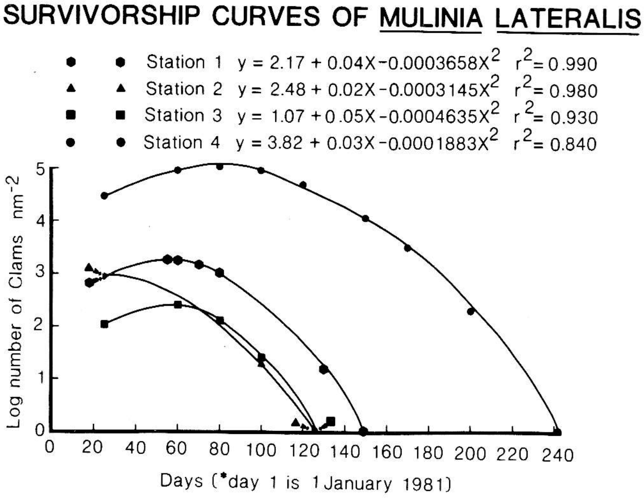

Figure 2. Survivorship curves for *Mulinia lateralis* at Stations 1 through 4. Day one is 1 January 1981.

a high of 63,168 • m^{-2} at Sta 4 in February. From January to March, individuals declined from 63,168 to 17,346 • m^{-2} at Sta 4; similar declines occurred at the other stations from February to April.

Histograms show changes in clam size with time and because there was only a single set, cohort production at the four stations could be estimated (Fig. 3).

The regression equation of shell length (SL) in cm to mean dry weight (DW) in grams is:

$$\text{g DW} = 0.01095\,(\text{SL cm})^{2.968},\ r^2 = 0.94$$

and compares well to other bivalves (Winberg 1971). Changes in biomass with time were examined by the equation:

$$\bar{w} = at^b$$

where $\bar{w}$ = mean dry weight and t = time in days from settlement at each of the stations. The estimate of initial settlement was the beginning of January. By using monthly data points, the prediction was made by varying the day of settlement until the highest correlation coefficient was obtained. The best fit (r^2 = 0.99) was obtained when 1 or 2 January was used as the day of initial settlement.

Exponential growth rates were highest at Sta 3 and lowest at Sta 4 (Fig. 4). Slow individual growth rates at Sta 4 probably resulted from the high clam densities at that station.

Cohort production, standing crop, and cohort turnover ratios varied from a high production value of 325 g DW • m^{-2} • 7 mo^{-1} with a high standing crop of 513.44 g DW • m^{-2} at Sta 4 to a low production value of 0.29 g DW • m^{-2} • 4 mo^{-1} and low standing crop of 0.60 g DW • m^{-2} at Sta 2.

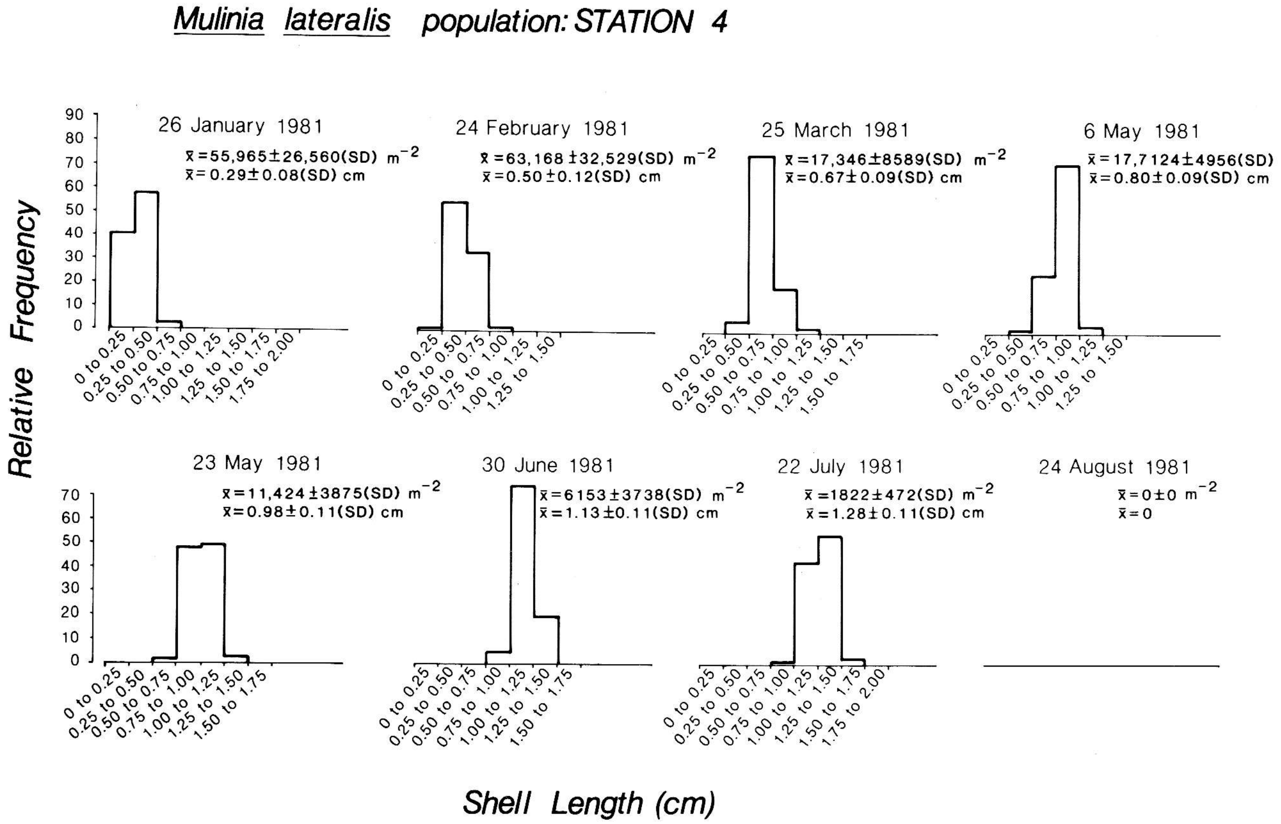

Figure 3. Monthly histograms for Station 4 showing changes in number • m^{-2}, average size, and the formation of only one cohort.

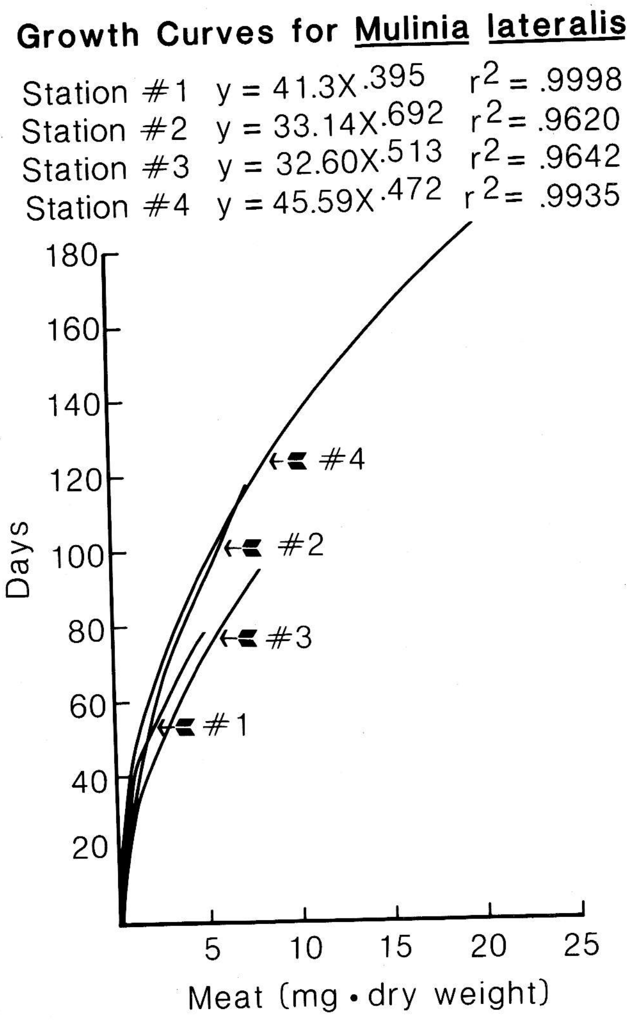

Figure 4. Growth rates for *Mulinia lateralis* at Stations 1 through 4.

Cohort production was estimated at 7.3 g DW $\cdot$ m^{-2} $\cdot$ 3 mo^{-1} with a standing crop of 9.19 g DW $\cdot$ m^{-2} and 4.12 g DW $\cdot$ m^{-2} $\cdot$ 4 mo^{-1} with a standing crop of 8.05 g DW $\cdot$ m^{-2} at Sta 1 and 3, respectively. Cohort turnover rates (P/B) ranged from a low of 1.93 for Sta 2 to a high of 4.40 for Sta 4 with Sta 1 and 3 having ratios of 2.38 and 2.05, respectively. The differences in estimates were attributed to differences in densities in clams. The higher the densities, the higher the production, standing crop, and turnover ratio (Table 1).

DISCUSSION

Salinity is a major regulator of benthic populations (Wells 1961) and year-to-year excessive salinity depression in winter/spring appears to regulate the annual recruitment of *M. lateralis* in Wassaw Sound. Low salinity (< 20 ppt) occurred during the winters from 1977 to 1980, during the period of normal reproduction which could affect gamete and larval development and survival. Larval development of *M. lateralis* is most successful (> 70%) from 22.5 to 30 ppt but can occur as low as 15 ppt (Calabrese 1969). Larval survival and growth is optimum at 20 to 27.5 ppt.

TABLE 1

Cohort production by instantaneous growth method, cohort turnover ratio, mean density of clams for duration of population, and the duration of the population for Stations 1 through 4. Cohort production is in grams dry weight m^{-2} per duration of the population.

	Cohort* Production	Cohort* P/$\overline{B}$	Mean* Monthly Density (± SD)	Duration of Population
Station 1	7.29	2.38	1437±304	January to March
Station 2	0.29	1.93	148±252.6	January to April
Station 3	4.12	2.05	462±517	January to April
Station 4	325.28	4.44	24,770±24,540	January to July

* Based on less than one year, i.e., 3 mo for Sta 1, 4 mo for Sta 2 and 3, and 7 mo for Sta 4.

The distribution of animals within estuarine systems is generally related to salinity (Wells 1961, Menzel 1964, Wass 1965). Other environmental factors associated with salinity reductions, however, could be responsible for the lack of successful annual recruitment of *M. lateralis* in Georgia. For instance, with heavy freshwater runoff, a major shift in water mass could affect larval transport and settlement as well as changes in primary production. Furthermore, heavy runoff could increase the amount of suspended sediments as well as alter bottom sediments. Davis (1960) showed that growth and survival of clam (*Mercenaria mercenaria*) eggs and larvae was correlated to the type and concentration of various suspended material. Instability of the bottom surface can result in clogged filtering structures of suspension feeders, burying newly settled larvae or discouraging settling of suspension feeding bivalves (Rhoads and Young 1970).

Total cohort production was 100 times greater at Sta 4, located in the more saline region of the outer Sound, than at Sta 1 and 3 in the inner Sound. Further, Sta 1 and 3 were 24 and 14 times, respectively, more productive than Sta 2 located in the area of lowest salinity. This resulted from clam density and duration of the various populations. Clams at Sta 4 were dense and survived for 7 mo, while those at Sta 2 had a low density and survived 4 mo.

Populations of *M. lateralis* were quickly decimated following a heavy set in January 1981. Mortality probably resulted from predation by blue crabs *Callinectes sapidus* Rathbun. An abundance at all stations of shell fragments characteristic of crab predation (MacKenzie 1977) suggested heavy predation by the blue crab, a major predator of adults of *M. lateralis* (Virnstein 1977). Mortality of *M. lateralis* also resulted from the moon snail *Polinices duplicatus* (Say) as determined by type of bore hole (Carriker 1951), accounted for a small percentage of the monthly losses at Sta 4. Mean clam mortalities caused by snails were: 0, 504, 231, and 1008 clams $\cdot$ m^{-2} in February, March, April, and May,

TABLE 2

Annual production and P/B ratios of species of bivalves (production in g Ash Free Dry Weight m^{-2} unless otherwise stated). Bivalve age is in years.

Species	Production g AFDW m^{-2} yr^{-1}	$P/\bar{B}$ (yrs.)	Max. Age	Locality	Reference
Geukensia demissus* (Dillwyn)	3.34	?	0.28	Georgia, U.S.A.	Keunzler 1961
Tagelus divisus (Spengler)	21.0 g DW	1.78	2	Biscayne Bay, FL	Fraser 1967
Tellina martinicensis (Orbigny)	0.23 g DW	2.40	2	Biscayne Bay, FL	Penzias 1969
Chione cancellata (Linné)	8.90 g DW	0.42	7	Biscayne Bay, FL	Moore & Lopez 1969
Dosinia elegans (Conrad)	0.13 g DW	1.25	2	Biscayne Bay, FL	Moore & Lopez 1970
Anodontia alba (Link)	14.09 g DW	1.43	?	Biscayne Bay, FL	Moore & Lopez 1972
Mya arenaria (Linné)	11.60 g DW	2.54	3	Petpeswich Inlet, Can.	Burke & Mann 1974
Mya arenaria (Linné)	2.66	0.5	8	Lynher Estuary, U.K.	Warwick & Price 1975
Scrobicularia plana (da Costa)	0.48	0.20	9	Lynher Estuary, U.K.	Warwick & Price 1975
Macoma balthica (Linné)	0.31	0.90	6	Lynher Estuary, U.K.	Warwick & Price 1975
Macoma balthica (Linné)	1.93 g DW	1.53	3	Petpeswich Inlet, Can.	Burke & Mann 1974
Macoma balthica (Linné)	3.40	1.93	8.10	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
Macoma balthica (Linné)	0.94	1.00	8.10	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
Ensis siliqua (Linné)	1.37	0.27	10	Carmarthen Bay, South Wales	Warwick et al. 1978
Cerastoderma edule (Linné)	0.21	0.20	7	Lynher Estuary, U.K.	Warwick & Price 1975
Cerastoderma edule (Linné)	29.25	1.59	5	Southampton Waters, U.K.	Hibbert 1976
Cerastoderma edule (Linné)	71.36	1.10	5	Southampton Waters, U.K.	Hibbert 1976
Cerastoderma edule (Linné)	46.44	2.61	5	Southampton Waters, U.K.	Hibbert 1976
*Cerastoderma** edule* (Linné)	10.21	0.69	3.5	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
*Cerastoderma** edule* (Linné)	119.82	2.59	3.5	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
*Cerastoderma** edule* (Linné)	51.76	1.13	3.5	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
Venerupis aurea (Gmelin)	0.70	1.11	5	Southampton Waters, U.K.	Hibbert 1976
Venerupis aurea (Gmelin)	1.25	1.10	5	Southampton Waters, U.K.	Hibbert 1976
Venerupis decussata (Linné)	0.21	0.52	?	Southampton Waters, U.K.	Hibbert 1976
Venerupis decussata (Linné)	0.60	0.28	?	Southampton Waters, U.K.	Hibbert 1976
Donax vittatus (da Costa)	0.72	2.10	2.5	Carmarthen Bay, South Wales	Warwick et al. 1978
Venus striatula (da Costa)	0.62	0.41	10	Carmarthen Bay, South Wales	Warwick et al. 1978
Tellina fabula (Gmelin)	0.29	0.90	6	Carmarthen Bay, South Wales	Warwick et al. 1978
Tellina deltoides	2.35	1.42	4	Westernport Bay, Australia	Robertson 1979
Abra alba (Wood)	1.45	2.0	1.2	Concarneau Bay, France	Glemarec and Menesquen 1980
Crassostrea virginica (Gmelin)	4132 Kcal	2.01	2	South Carolina, U.S.A.	Dame 1976
Mytilus edulis (Linné)	3.68	1.00	?	Southampton Waters, U.K.	Hibbert 1976
Mytilus edulis (Linné)	4.82	1.00	?	Southampton Waters, U.K.	Hibbert 1976
Mytilus edulis (Linné)	29.43 KJ y^{-1}	?	7	Lynher Estuary, U.K.	Bayne & Worrall 1980
Mytilus edulis (Linné)	14.40 KJ y^{-1}	?	7	Cattewater Estuary, U.K.	Bayne & Worrall 1980
Mytilus edulis (Linné)	790.0	?	1	Nyckelbyviken Bay, Sweden	Loo & Rosenburg 1983
Mytilus edulis (Linné)	648.0	?	1	Nyckelbyviken Bay, Sweden	Loo & Rosenburg 1983
Mytilus edulis (Linné)	476.0	?	1	Nyckelbyviken Bay, Sweden	Loo & Rosenburg 1983
Mulinia lateralis (Say)	7.29 DW	2.38	0.25	Georgia, U.S.A.	This study
Mulinia lateralis (Say)	0.29 DW	1.93	0.33	Georgia, U.S.A.	This study
Mulinia lateralis (Say)	4.12 DW	2.05	0.33	Georgia, U.S.A.	This study
Mulinia lateralis (Say)	325.28 DW	4.44	0.58	Georgia, U.S.A.	This study
Mercenaria mercenaria (Linné)	62.82	3.02	1	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	23.71	1.85	1	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	133.60	3.38	1	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	0.51	0.25	9	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	6.15	0.18	34	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	18.53	0.17	30	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	0.24	0.25	9	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	6.57	0.19	34	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	6.49	0.22	30	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	3.99	0.52	8	Southampton Waters, U.K.	Hibbert 1976
Mercenaria mercenaria (Linné)	14.00	0.28	8	Southampton Waters, U.K.	Hibbert 1976
Mercenaria mercenaria (Linné)	6.19	0.17	9	Southampton Waters, U.K.	Hibbert 1976

* Given as *Modiolus demissus* in Keunzler (1961).

** Given as *Cardium edule* in Wolff and deWolf (1977).

TABLE 3

Some literature values for annual production (values in g Ash Free Dry Weight) of marine communities.

Locality	Production g AFDW • m^{-2} • yr^{-1}	Source
Long Island Sound, U.S.A.	8.0 to 64.5	Sanders 1956
Lynher Estuary, U.K.	13.3	Warwick & Price 1975
Southampton Waters, U.K.	220.0	Hibbert 1976
Grevelingen Estuary, Netherlands	0.1 to 219.9	Wolff & deWolf 1977
Carmarthen Bay, South Wales	25.8	Warwick et al. 1978

respectively. These values represented 0, 1.1, < 1, and 16% of total mortality. The spot *Leiostomus xanthurus* Lacepède is also a major predator of *M. lateralis* (Virnstein 1977); those caught in June had been feeding primarily on *M. lateralis* (personal observations).

Production estimates of *M. lateralis* ranged from 0.3 g DW • m^{-2} • 4 mo^{-1} to 325 g DW • m^{-2} • 7 mo^{-1} and are comparable to production data for other bivalves (Table 2) and benthic communities (Table 3). Cohort turnover ratios were considerably higher in Wassaw Sound, however, than those cited for other bivalves because the population studied was comprised only of young individuals. Turnover ratios decreased with increase in age of organisms (Nichols 1975, Warwick 1980, Walker 1984). The short-term production rate, i.e., the rate for the 3 to 7 mo that *M. lateralis* was present, was higher than reported for other bivalves. Thus, at least for a short period of time, *M. lateralis* effectively exploits available food resources and in turn can be a significant source of food for predators; however, year-to-year variations in production that resulted from recruitment failure that were caused by low winter salinities also caused a significant instability in the availability of this clam to predators.

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